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EMPIDONAX TRAILLII EXTIMUS: AN ENDANGERED SUBSPECIES

PHILIP UNITT, 3411 Felton Street, San Diego, California 92104

The Willow Flycatcher (*Empidonax traillii*) is a widely distributed species with a breeding range extending from southern British Columbia south to northern Baja California and east to the Atlantic coast. Small passerines with such wide ranges usually show some geographic variation, and several subspecies of *E. traillii* have been described by Oberholser (1918, 1932, 1947), Phillips (1948), and Aldrich (1951). But proof that the former "Traill's Flycatcher" is composed actually of two sibling species (Stein 1958, 1963), now known as the Willow and Alder (*E. alnorum*) flycatchers, disrupted the study of intraspecific variation in this pair. Mayr and Short (1970) wrote "we consider these species monotypic in view of their variability and difficulties in determining the specific, let alone subspecies, status of individual birds." Traylor (1979) likewise recognized no subspecies of *E. traillii*, but wrote "both species are almost certainly polytypic, but the subspecies cannot be worked out without long series of fresh material of known song type."

The problem of intraspecific variation in *E. traillii* is especially acute in view of the precarious status of the populations breeding in the southwestern United States, where the birds are restricted to riparian woodland. Although the species remains common east of the Mississippi, Garrett and Dunn (1981) considered the breeding population of southern California "virtually extirpated." In Arizona, Monson and Phillips (1981) noted that no nests were found between 1970 and 1981.

My purpose in this paper is to integrate the intimately related problems of the taxonomy, distribution, current status, reproductive biology, and conservation of the southwestern populations of *E. traillii*, with an emphasis on those in southern and Baja California.

TAXONOMIC PROCEDURES

Specimen Resources

To study geographic variation and migration of *E. traillii* in southern and Baja California, I examined 305 study skins: 60 in the San Diego Natural History Museum (SD), 126 in the Museum of Vertebrate Zoology, Berkeley (MVZ), 20 in the San Bernardino County Museum (SBCM), 15 from the

University of California, Los Angeles (UCLA), 16 from the Los Angeles County Museum (LACM), 10 from the University of Arizona (UA), 5 from the New York State Museum (NYSM), 50 from the United States National Museum (US), and one from the collection of Amadeo M. Rea (AMR).

Specimen Analysis

The first step necessary in analyzing geographic variation in breeding populations of E. traillii is to segregate specimens that were on their breeding territories when collected from those taken in migration. Ideally, this segregation should be made on the basis of a specimen label providing data on gonad development, fat condition, habitat, behavior, and song. Unfortunately, however, few labels on Willow Flycatchers bear this information; scientific collecting of birds declined about the time most ornithologists realized the importance of preserving such data with specimens. Therefore, I assumed that specimens collected from 24 June to 17 July, when Willow Flycatchers have not been reported migrating through the southwestern United States, also were on their breeding territories. In samples of specimens collected near the northern limit of the Willow Flycatcher's range, the likelihood of encountering birds far from their breeding range is low, so I assumed that all specimens from Oregon, Washington, and Idaho represented the breeding populations of the sites where they were collected. In the central and eastern United States the Alder Flycatcher migrates throughout the Willow Flycatcher's range, so from this area I used only specimens known to be traillii on the basis of song or that had been identified as such by R. C. Stein.

I examined these specimens for evidence of geographic variation in measurements, wing structure, and color. Measurements I took were wing chord, tail length from insertion of central rectrices, bill length from nostril, and bill width at base. From these data I calculated for each specimen wing length minus tail length, the ratio of wing length to tail length, and the ratio of bill length to bill width. I measured only adults, excluded measurements of structures that were badly worn or damaged by shot, and compared the sexes separately. I measured only the specimens in the SD, AMR, UA, NYSM, and US collections.

Phillips (1944) and Snyder (1953) reported that the eastern and western populations of *E. traillii* differ in wing formula, that the tenth primary is equal to or shorter than the fifth in western populations, longer in eastern. I examined the relative lengths of the fifth and tenth primaries in the same sample of specimens that I measured. Again, I compared the sexes separately, because I observed that within each population the wings of males average slightly more pointed than those of females.

Evaluation of Willow Flycatcher coloration requires more careful analysis than evaluation of size and structure. Age, length of time since collection, and degree of plumage wear are additional complicating factors contributing to color variation. Not all specimens suitable for measuring were suitable for color comparison.

An understanding of the species' molt schedule is essential to an understanding of the effects of age and wear on the birds' coloration. Willow Flycatchers have a single annual molt, which takes place in their winter range, after the birds have migrated south of the United States. Therefore, they are

in their freshest plumage when they arrive in the spring, wear during the breeding season, and are badly worn when they depart in the fall. Young birds migrate while still in their juvenal plumage, and return the following spring in a plumage identical to that of older adults. That is, the first basic plumage is definitive.

Juvenal Willow Flycatchers differ from adults by their buff wing bars and flimsy-textured plumage, which wears and fades much faster than the adult plumage.

Foxing, the change in plumage color that affects aging study skins, occurs in *E. traillii*. Foxing is manifested in *E. traillii* as a buff-brown tint to the greenish-gray parts of the plumage. It is usually slight, but I have noticed it in specimens collected as recently as the 1950s. The skins prepared by some collectors, particularly Frank Stephens, have foxed more than others. Therefore, the possibility of foxing must be considered when recently collected specimens are compared with older ones.

Plumage wear also affects the birds' appearance, particularly on the crown, where in extremely worn individuals the greenish distal portion of the feathers may be completely lost, leaving only the dark gray bases. Therefore, it is essential that worn birds not be compared with fresh ones and that conclusions be drawn from the least worn specimens possible.

Phillips (1948) reported that in *E. t. brewsteri* males average darker than females, and that in *E. t. extimus* males average more olive than females, but sexual differences are negligible in the specimens I examined. I therefore combined the sexes when comparing colors.

A Standard for Definition of the Subspecies

One definition of subspecies that ornithologists traditionally have used is the "75% rule": For population A to be considered a subspecies distinct from population B, 75% of the individuals of population A should overlap with no more that 3% of the individuals of population B (Mayr 1969). I have selected this purely morphological definition for characterizing the subspecies of E. traillii because it is more restrictive than the statistical significance of differences between population means, also used in some taxonomic studies. The 75% rule allows more individual specimens to be assigned to subspecies and is more easily applied to the characters in which the populations of E. traillii show the most external difference. Genetic definitions of subspecies have been introduced recently (Zink 1986) but genetic techniques were not available to me and would require the collection of more additional specimens than is currently practical.

If the variation in a mensural character is normally distributed, the 75% criterion can be expressed mathematically by

$$x_A + 0.675s_A > x_B - 1.88s_B$$

where x represents the mean, s the standard deviation, and $x_A < x_B$. The factors 0.675 and 1.88 derive from the table of z values of the normal distribution. If the standard deviations of the two populations are different, this test may not give the same results when B is compared to A as when A is compared to B. I therefore performed the test in both directions between each pair of subspecies in each character.

TAXONOMIC RESULTS

The most comprehensive study of geographic variation in *E. traillii* was by Aldrich (1951), who recognized five subspecies: *E. t. brewsteri* Oberholser (1918), breeding from the Pacific Ocean east to the Cascade Range and Sierra Nevada, *E. t. adastus* Oberholser (1932), breeding between the Cascades and the Rocky Mountains, *E. t. extimus* Phillips (1948), breeding in the desert Southwest, southern Great Basin, and "the southern Great Plains" (though breeding Willow Flycatchers are very rare to absent in that region), *E. t. traillii* (Audubon 1828), breeding from Alaska through the boreal forest of Canada to the northeastern United States, and *E. t. campestris* Aldrich (1951), breeding from the Great Plains east through the Great Lakes states. Subsequently, Stein (1958, 1963) demonstrated that Aldrich's nominate *traillii* is the separate species now known as the Alder Flycatcher, and Snyder (1953) and the A. O. U. Committee on Classification and Nomenclature (A. O. U. 1973) suggested that Audubon's name *traillii* is better applied to the Willow Flycatcher.

Measurements and Proportions

Measurements and proportions of the four subspecies of E. traillii are listed in Tables 1 and 2. The sharpest distinctions in size or proportion among the subspecies of E. traillii are the functions of wing and tail lengths. In males, the greatest difference is in the wing — tail difference between extimus and traillii, but in even that character the 75% rule is satisfied in only one direction of comparison. In females, traillii might be distinguishable from the three western subspecies in both wing — tail difference and wing/tail ratio. The 75% criterion is met in both directions when traillii is compared to brewsteri, and in one direction when traillii is compared to extimus or adastus. However, the sample of female traillii is so small (n=4) that any conclusion drawn from it can be considered only tentative. Therefore if subspecies exist in E. traillii they must be defined on a basis other than size.

Color

My results with respect to plumage color and wing structure, however, accord for the most part with those of Aldrich (1951) and Snyder (1953). The back color in specimens 40 to 80 years old (the great majority of those available) of all four subspecies is close to Olive (color 30) of Smithe (1975) but somewhat greener. In brewsteri the green is in the direction of Olive Green (color 48), in adastus in the direction of Greenish Olive (color 49), and in extimus and traillii in the direction of Grayish Olive (color 43). That is, brewsteri is a dark brownish olive, adastus a dark grayish green, and extimus and traillii a pale gravish green. In less worn individuals the contrast between a paler cap and darker back often noticeable in brewsteri and adastus is usually lacking in extimus and traillii. In extimus and traillii the underparts as well are often paler than in brewsteri and adastus, and the grayish breast band is less distinct, but these differences are less constant than those on the upperparts. I saw no consistent differences in color between extimus and traillii and cannot confirm Aldrich's (1951) statement that "campestris" (i. e., traillii) is "somewhat more greenish" than extimus. The sample of "traillii" with which

Table 1 Measurements and Proportions of Male Empidonax traillii

	extimus*	traillii	adastus ^c	brewsteri ^a
Wing chord	_			
n	9	10	25	22
Mean	68.7	70.8	70.4	68.0
Range	65.7-72.5	68.8-74.2	66.8-73.9	65.9-71.2
SD.	2.04	1.73	1.68	1.35
Tail length				
n	9	9	25	22
Mean	59.3	59.1	59.7	58.1
Range	56.8-62.5	56.3-62.6	56.4-62.7	54.8-60.7
SD	1.91	1.96	1.57	1.61
Wing minus	tail			
n	9	9	25	22
Mean	9.4	11.9	10.6	9.9
Range	7.9-11.6	10.6-12.8	8.4-13.4	7.5-12.5
SD	1.26	0.71	1.04	1.14
Wing/tail rati	io			
n	9	9	25	22
Mean	1.16	1.20	1.18	1.17
Range	1.13-1.20	1.18-1.22	1.14-1.23	1.13-1.22
SD	0.023	0.016	0.019	0.023
Bill length fro	om nostril			
n	9	10	24	21
Mean	9.7	9.2	9.5	9.5
Range	9.2-10.2	8.9-9.7	8.6-10.2	8.5-10.0
SD	0.32	0.25	0.37	0.36
Bill width at	base			
n	9	10	25	22
Mean	7.1	7.2	7.2	7.3
Range	6.7-7.5	6.7-7.8	6.5-8.1	6.8-8.0
SD	0.26	0.36	0.41	0.34
Bill length/w	idth ratio			
n S.	9	10	24	21
Mean	1.37	1.27	1.32	1.31
Range	1.29-1.50	1.18-1.39	1.14-1.48	1.18-1.44
SD	0.069	0.060	0.085	0.063

*Localities represented: Calif., Imperial Co., Potholes (4); Baja Calif. Norte, Las Cabras (2); Ariz., Navajo Co., ½ mi. E Fort Apache (1); Pinal Co., 9 mi. S Mammoth (1); Pima Co., Tucson (1). *Localities represented: N. Dak., Ward Co., Kenmare (1); Kidder Co., Dawson (1); Dickey Co., Oakes (2); S. Dak., Miner Co. (1); N. Y., Monroe Co., Hilton (1); Tompkins Co., Ithaca (4). *Localities represented: Wash., Okanagan Co., Riverside (1); Lincoln Co., Sylvan Lake (1), Sprague Lake (1), 6 mi. S Sprague (1); Spokane Co., Spokane (1); Whitman Co., Pullman (1), Uniontown (2); Asotin Co., Anatone (1), Grande Ronde River (1); Ore., Umatilla Co., Pendleton (1); Wallowa Co., Swamp Creek (1); Baker Co., Homestead (1); Harney Co., Stinking Water Mt. (1); Malheur Co., Beulah (1), 3 mi. W Juntura (2), Rockville (1); Nev., Washoe Co., Reno (1); Pershing Co., Winnemucca Lake (1); Ida., Boundary Co., Porthill (1); Butte Co., Big Lost River (1); Utah, Davis Co., Antelope Island (1); Carbon Co., Clear Creek (1); Mont., Flathead Co., Java (1).

^{**}Cocalities represented: Wash., Clallam Co., Forks (1); Ore., Multnomah Co., Portland (6); Marion Co., Salem (1), Scotts Mills (1); Calif., San Diego Co., La Jolla (1), Bonita (1), Ballena (1); Imperial Co., Potholes (5), Bard (2); Baja Calif. Norte, Ojos Negros (1); Ariz., Yuma Co., Yuma (1); Sonora, Isla Tiburon (1).

SD, standard deviation.

Table 2 Measurements and Proportions of Female Empidonax traillii

	extimus*	traillii	adastus	brewsteri ^a
Wing chord				
n	15	4	16	12
Mean	65.7	66.9	67.0	64.8
Range	62.7-70.1	65.8-68.2	64.4-69.4	61.3-69.3
SD	1.98	1.00	1.25	2.09
Tail length				
n	15	4	16	12
Mean	57.3	54.8	57.5	56.5
Range	54.5-60.2	53.1-56.7	55.7-59.5	55.0-59.8
SD	2.04	1.49	1.20	1.43
Wing minus ta	il			
n	15	4	16	12
Mean	8.4	12.1	9.5	8.2
Range	4.5-11.9	11.3-13.5	8.0-11.2	4.0-10.0
SD	1.90	0.99	1.05	1.58
Wing/tail ratio				
n	15	4	16	12
Mean	1.15	1.22	1.16	1.15
Range	1.08-1.20	1.20-1.25	1.14-1.20	1.07-1.18
SD	0.035	0.023	0.020	0.028
Bill length from	n nostril			
n	13	4	16	11
Mean	9.5	9.4	9.1	9.3
Range	8.7-10.1	9.0-9.6	8.5-10.0	8.8-9.8
SD	0.47	0.29	0.46	0.35
Bill width at ba	ase			
n	15	4	15	12
Mean	7.4	7.3	7.2	7.4
Range	6.8-7.9	7.2-7.4	6.7-7.6	6.8-8.0
SD	0.33	0.08	0.29	0.35
Bill length/wid	lth ratio			
n	13	4	15	11
Mean	1.30	1.29	1.27	1.25
Range	1.20-1.45	1.25-1.32	1.13-1.46	1.14-1.40
SD	0.075	0.031	0.088	0.071

*Localities represented: Calif., San Diego Co., Doane Valley (1), 3.6 km NW Lake Henshaw Dam (1), National City (1); Imperial Co., Potholes (2), Bard (2); Ariz., La Paz Co., Bill Williams Delta (1); Yuma Co., Yuma (6); Pima Co., Tucson (1).

^{*}Localities represented: N. Dak., Kidder Co., Dawson (2); Richland Co., Lidgerwood (1); Illinois, Fulton Co., Canton (1).

Localities represented: Wash., Lincoln Co., Sylvan Lake (1), 6 mi. S Sprague (1); Whitman Co., Palouse (1), Pullman (1); Ore., Wallowa Co., Enterprise (1), Swamp Creek (1); Baker Co., Homestead (1); Crook Co., 20 mi. S Paulina (1); Klamath Co., head of Whiskey Creek (1); Ida., Latah Co., Potlatch (1), Harvard (1), Moscow (1); Power Co., American Falls (1); Utah, Box Elder Co., Bear River mouth (1); Wyo., Stanley (not located; possibly Stansbury, Sweetwater Co., Wyo., or Stanley, Custer Co., Ida.) (1); N. Mex., Guadalupe Co., Santa Rosa (1). Localities represented: Wash., King Co., Seattle (1); Ore., Multnomah Co., Portland (4); Calif., Yolo Co., Grafton (1); San Diego Co., La Jolla (1); Imperial Co., Potholes (2), Bard (2); Baja Calif. Norte, Las Cabras (1).

Phillips (1948) compared extimus consisted largely if not entirely (A. R. Phillips pers. comm.) of alnorum, which is usually if not always darker and greener than even adastus (pers. obs. of specimens in NYSM and US).

One hundred percent of specimens of extimus from the lower Colorado River and Arizona are paler and grayer on the back than all specimens of brewsteri. For specimens from southwestern California and northwestern Baja California, the figure drops to 82%. Eighteen of 20 specimens (90%) from Arizona, southern California, and northern Baja California that should have been extimus on the basis of range are paler-backed than adastus, while 26 of 28 specimens (93%) from eastern Washington, eastern Oregon, northern Nevada, Idaho, northern Utah, and Wyoming are darker than extimus. Twenty-five of 28 adastus (89%) are grayer or purer green than brewsteri, while 15 of 18 brewsteri (83%) are browner or more olive than adastus.

Wing Formula

Phillips (1944) and Snyder (1953) reported that the eastern and western populations of *E. traillii*, as then considered, differ in wing formula, that in eastern birds, the tenth primary is longer than the fifth, while in the western birds, the tenth is equal to or shorter than the fifth. My results (Table 3) support this conclusion. The wing formula thus distinguishes 93% of the *extimus* and *traillii* in my sample, 88% of the *adastus* and *traillii*, and 89% of the *brewsteri* and *traillii*. It is more reliable for females than for males; the western

Table 3 Relative Lengths of Primaries 10 and 5 in the Four Subspecies of *Empidonax traillii**

	10 > 5		10 = 5		10 < 5	
	n		n		n	%
Males			·			
traillii	20	95	1	5		
extimus	3	18	4	24	10	59
adastus	9	20	19	41	18	39
brewsteri	7	17	18	45	15	38
Females						
traillii	6	86			1.	14
extimus			3	11	24	89
adastus	1	4	8	31	17	65
brewsteri	_		2	8	22	92

^{*}Each individual wing scored separately; wings with primaries 10 or 5 broken or badly worn not scored. Of 93 specimens with primaries 5 and 10 intact on both sides, 11 were sufficiently asymmetrical that the two wings fell into different categories. All cases of asymmetry, however, included the 10=5 category; that is, in no case was 10>5 in one wing and 10<5 on the other. Asymmetry was most frequent in adastus (7 of 34 specimens).

^{*}Specimen poorly prepared, with wings apparently tied to body, so primary formula possibly disrupted.

birds in which the tenth primary is longer than the fifth are mostly long-winged males (wing chord > 70 mm).

Summary

I conclude that the four races of *E. traillii* recognized by Aldrich (1951) are valid by the criterion of the 75% rule and may be distinguished from each other by color, wing formula, or both. Figure 1 shows the approximate original breeding ranges of all four subspecies of *E. traillii* plus that of *E. alnorum*. The morphological differences among the races of *E. traillii* are minor, but differ little in magnitude from those distinguishing the species traillii from alnorum. In *Empidonax*, small differences in morphology may mask large differences in biology.

My concern in this study is the Willow Flycatchers of the southwestern United States and therefore with *E. t. extimus*. Although *E. t. extimus* was omitted from the 1957 edition of the A. O. U. Check-List of North American Birds, it has been recognized in all taxonomic studies of *E. traillii* since its original description. Its existence has been generally unappreciated probably because migrants of other subspecies occur commonly in its range during most of its breeding season, because of the dearth of original research on subspecies during the last 30 years, and because of fear of confusion of *E. traillii* with the sibling species *E. alnorum*, which does not occur in the southwestern states. During this period of neglect, *extimus* has dwindled nearly to extinction as the habitat on which it depends has been degraded and decimated.

Empidonax traillii extimus in California

Phillips (1948) and Aldrich (1951) included southern California in the breeding range of brewsteri, but my study shows that instead extimus occupies this area. All southern and Baja California specimens that either were labeled as breeding or were collected from 20 June to 15 July are listed in Table 4. These data indicate that only race extimus breeds in southern and Baja California and that intergradation with the subspecies to the north begins around Independence and Los Angeles. All specimens from Mono and northern Inyo counties are adastus or migrant brewsteri, so I suggest that Independence represents the northern limit of the range of extimus in eastern California. Three probably breeding specimens (MVZ) from the Sierra Nevada of Fresno County were all brewsteri, so it seems reasonable to regard Weldon as the northern limit of extimus along the axis of the Sierra Nevada. A single specimen (US 264166) collected at Tulare Lake 9 miles south of Lemoore, Kings County, on 20 June 1907 is too worn and poorly prepared to identify. I could find no specimens that unquestionably represent the population of coastal central California, so the northern limit of extimus along the coast is uncertain. However, no specimens of extimus have been collected in coastal California north of the San Fernando Valley.

New Specimen

Table 4 makes it obvious that the number of specimens of breeding Willow Flycatchers from southern California is small. Because only a small sample, or even a single individual, is preserved from most localities, further specimens

would be desirable to support the conclusion that *extimus* is the subspecies breeding in southern California. Since the populations remaining in southern California are now so small and few, such collecting must be done judiciously, preferably from the largest remaining colonies. The only suitable site where I was able to collect is along the San Luis Rey River 3.6 km northwest of the Lake Henshaw dam in the Cleveland National Forest, San Diego County, where I obtained one female on 21 May 1984. The specimen, my original number 375, is now SD 44653. Its ovary was beginning to enlarge (7.5 × 4 mm, largest ovum 1.5 mm diameter) and it had only slight fat, indicating that it was on its breeding territory but had not yet begun to nest. This specimen is clearly *extimus*, on the basis of comparison with other unfoxed specimens, as it matches closely one collected at Fort Apache, Arizona, on 29 May 1972 (AMR 3915) but is much paler than a migrant *brewsteri* found dead at Borrego Springs, San Diego County, on 1 June 1980 (SD 42124).

Although the concept of the occurrence of *extimus* in California rests on a small number of specimens, there is little likelihood that this base can be added to soon. Therefore, the range of the subspecies must be estimated on

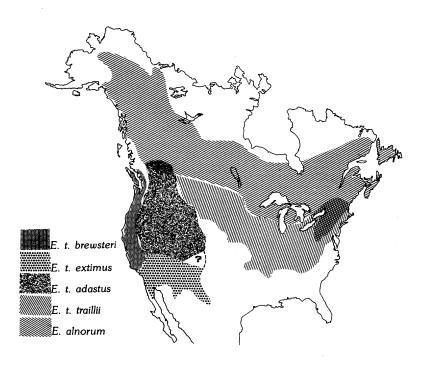


Figure 1. Breeding ranges of the subspecies of E. traillii and of E. alnorum.

Table 4 Southern and Baja California Specimens of Willow Flycatcher Labeled as Breeding or Collected from 20 June to 15 July

בי ביווים וכי דים ממוא				
Specimen number	Locality	Date collected	Indication of breeding on specimen label	Subspecies
MVZ 29766	2 mi. N of Independence, Inyo Co.	28 Jun 1917	"breeding"	extimus
MVZ 27967	2 mi. N of Independence, Inyo Co.	28 Jun 1917	"breeding"	brewsteri
MVZ 19993	Weldon, Kern Co.	5 Jul 1911	none	extimus
MVZ 40543	Oro Grande, San Bernardino Co.	26 May 1920	"testes large"	extimus
LACM 7015	Cienaga (= West Los Angeles), Los Angeles Co.	21 Jun 1889	none	extimus
LACM 7012	El Monte, Los Angeles Co.	20 Jun 1903	none	extimus/ brewsteri intermediate
LACM 7013	El Monte, Los Angeles Co.	20 Jun 1903	none	specimen too dirty to identify
LACM 7017	El Monte, Los Angeles Co.	20 Jun 1903	none	extimus
MVZ 136340	Rivera, Los Angeles Co.	9 Jul 1920	none	extimus
LACM 22295	Los Cerritos, Los Angeles Co.	12 Jun 1908	"breeding"	extimus
LACM 22296	Los Cerritos, Los Angeles Co.	12 Jun 1908	"breeding"	specimen too poorly prepared to identify

Table 4 (Continued)

Specimen number	Locality	Date collected	Indication of breeding on specimen label	Subspecies
SBCM 36127	Colton, San Bernardino Co.	26 Jun 1918	nest and eggs collected with specimen	extimus/ brewsteri intermediate
LACM 66116	Capistrano Beach, Orange Co.	8 Jul 1966	testes "enlarged"	extimus
LACM 66117	Capistrano Beach, Orange Co.	8 Jul 1966	none	specimen too dirty to identify
SD 31867	National City, San Diego Co.	5 Jun 1913	"inc[ubating]"	extimus
SBCM 36116	3 mi. W of Niland, Imperial Co.	13 Jun 1953	"testes 5 mm"	extimus (specimen foxed)
SD 13233	Potholes (= Laguna Dam), Imperial Co.	26 Jun 1930	none	extimus
SD 17825	Potholes (= Laguna Dam), Imperial Co.	22 Aug 1938	"feeding grown young"	extimus
SD 9903	La Grulla, Sierra San Pedro Martir, Baja California	27 Jun 1925	"breeding"	extimus

the basis of the currently available specimens. All identifiable southern California specimens labeled as breeding or collected between 13 June and 17 July are *extimus* except for the two intermediates from El Monte and Colton listed in Table 4.

Table 5 Additional Southern and Baja California Specimens of *Empidonax traillii extimus* (No Indication of Breeding on Specimen Label)

Specimen number	Locality	Date		Age
MVZ 27965	Wild Rose Canyon, Panamint Mts., Inyo Co.	12 Jun 19		ad.
LACM 7011	San Fernando, Los Angeles Co.	13 Jun 18		juv.
MVZ 33378	San Fernando Valley, Los Angeles Co.	13 Sep 19		juv.
LACM 7016	Cienaga (= West Los Angeles), Los Angeles Co			juv.
MVZ 33375	El Monte, Los Angeles Co.	12 Aug 18		juv.
UCLA 23810	Long Beach, Los Angeles Co.	10 May 19		ad.
MVZ 33381	Seven Oaks, San Bernardino Co.	13 Jun 19		ad.
MVZ 3187	Santa Ana R. near Colton, San Bernardino Co.	20 Jul 19		ad.
MVZ 3182	Santa Ana R. near Colton, San Bernardino Co.	25 Jul 19		juv.
MVZ 11753	Riverside, Riverside Co.	26 Jul 18		juv.
MVZ 11755	Riverside, Riverside Co.	26 Jul 18		juv.
MVZ 3078	Palm Canyon, San Jacinto Mts., Riverside Co.	12 Jun 19		ad.
SD 19184	Doane Valley, Palomar Mts., San Diego Co.	12 Jun 19	945	ad.
UCLA E128	Sunnyside, Sweetwater R., San Diego Co.	6 Jun 19	917	ad.
MVZ 3615	Campo, San Diego Co.	13 May 19	908	ad.
SBCM 36114	,	5 Oct 19		juv.
SBCM 36115	3 mi. W of Niland, Imperial Co.	13 Jun 19	953	ad.
SBCM 36117	3 mi. W of Niland, Imperial Co.	4 Sep 19		juv.
SBCM 36118	3 mi. W of Niland, Imperial Co.	4 Sep 19		juv.
SBCM 36119	3 mi. W of Niland, Imperial Co.	4 Sep 19	953	juv.
UCLA 31873	Salton Sea, Imperial Co.	26 May 19	934	ad.
SD 13037	Potholes (= Laguna Dam), Imperial Co.	5 May 19	930	ad.
SD 13038	Potholes (= Laguna Dam), Imperial Co.	5 May 19	930	ad.
SD 13200	1 mi. N of Potholes (= Laguna Dam), Imperial Co.	30 May 19	930	ad.
SD 13222	1 mi. N of Potholes (= Laguna Dam), Imperial Co.	10 Jun 19	930	ad.
SD 19164	Bard, Imperial Co.	3 Jun 19	945	ad.
SD 10019	2 mi. N of Bard, Imperial Co.	28 Sep 19	925	juv.
SD 13204	3 mi. N of Bard, Imperial Co.	31 May 19		ad.
MVZ 12910	Colorado River 5 mi. NE of Yuma, Imperial Co.	4 May 19	910	ad.
SD 8714	Las Cabras, Rio San Telmo, Baja California	4 Jun 19		ad.
MVZ 52932	7 mi. E of Cerro Prieto, Colorado delta	5 Jun 19	928	ad.
MVZ 52933	7 mi. E of Cerro Prieto, Colorado delta	6 Jun 19	928	ad.
MVZ 52934	7 mi. E of Cerro Prieto, Colorado delta	11 Jun 19	928	ad.
MVZ 52935	7 mi. E of Cerro Prieto, Colorado delta	11 Jun 1	928	ad.

DISTRIBUTION OF EMPIDONAX TRAILLII EXTIMUS

In addition to the museum study skins listed in Tables 4 and 5, I used the data cards accompanying the egg collections of SBCM and the Western Foundation for Vertebrate Zoology, Los Angeles (WFVZ), as my sources of information on the subspecies' original range in southern California. Literature reports of *Empidonax* species may be questioned in this genus of difficult-to-identify birds unless the identifications are supported by specimens still available for reexamination. Fortunately, however, published accounts of Willow Flycatchers in southern California do not deviate much from the evidence verifiable through preserved specimens.

My primary sources of information on the range of extimus east of California were Behle (1985) and a list of specimens identified and supplied by A. R. Phillips. I used published literature as a supplementary source for additional breeding localities within the range delineated by these sources. Egg collections, though a major information resource for coastal southern California, are nearly lacking from the region east of the Colorado River.

Breeding or probable breeding localities for the entire range of *extimus* are plotted in Figure 2, where crosses indicate localities where Willow Flycatchers were found before 1970 but have not been reported since.

California

Willett (1912, 1933) stated that Willow Flycatchers bred commonly in coastal southern California, and the large numbers of egg sets collected before 1940 in the Los Angeles basin (67), the San Bernardino/Riverside area (34), and San Diego County (42) bear this out. I have plotted egg records from the Santa Clara River in Ventura County also in Figure 2, although I have seen no unquestionably breeding specimens that would indicate the subspecific identity of that population. In southeastern California, substantial Willow Flycatcher populations probably existed only along the Colorado River, as indicated by 37 nests collected by Herbert Brown near Yuma in 1902, 33 of which are now in the University of Arizona (J. Bates and T. R. Huels, pers. comm.).

Baja California

The six specimens from the three Baja California localities listed in Tables 4 and 5 constitute all available information on the summer range of Willow Flycatcher in that region. Previously, the species' status in the peninsula had not been determined precisely. The specimen from La Grulla is the only evidence indicating that the Willow Flycatcher has ever nested in Baja California. The "almost certain" *E. traillii* reported from various locations in northern Baja California between 5 and 24 April 1967 (Short and Crossin 1967) were almost certainly misidentified because the species is unknown in southern California earlier than 28 April and does not normally winter north of southern Mexico.

Arizona

In the other parts of its range, which are largely desert, extimus was always localized and usually uncommon. It is known to have occurred at a few

localities along the San Pedro River, and one of these, Feldman, is its type locality. Other areas of known occurrence in Arizona were the Santa Cruz River near Tucson, Camp Verde, the Colorado River (Lee's Ferry and junction of Little Colorado River as well as along the California border), and the White Mountain region (Whiteriver, Springerville, and Alpine) (Phillips 1948 and pers. comm.; Phillips et al. 1964).

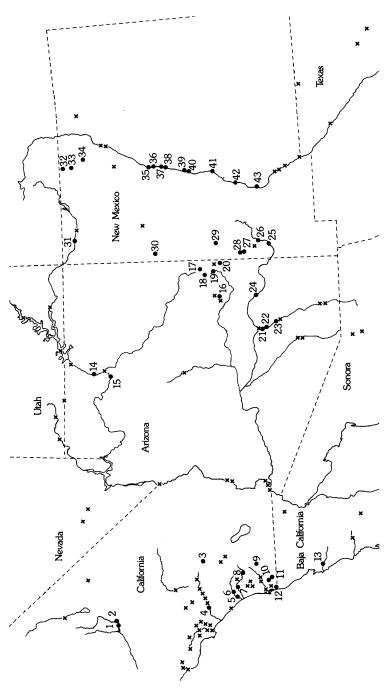
Nevada

E. t. extimus has been recorded at only three Nevada localities: Indian Springs (three nesting pairs in 1932, two specimens collected on 8 and 11 July, Linsdale 1936), Corn Creek (one specimen on 16 May 1962), and Colorado River at the southern tip of the state (one specimen on 9 May 1953, A. R. Phillips, pers. comm.).

Utah

The northern limits of extimus in the eastern part of its range have been subject to widely different interpretations. Snyder (1953) ascribed the subspecies to northeastern Utah, Burleigh (1972) to southern Idaho, and Aldrich (in Bailey and Niedrach 1965) to Colorado. Aldrich (1951) outlined its range rather vaguely as including the southern Great Basin and the southern Great Plains. The reason for these varying concepts is that the intergradation between extimus and adastus in the Great Basin/Rocky Mountain area is much more gradual than that between extimus and brewsteri in California, where the intermediate population, if any, in central California was never collected and is now extinct. Behle (1985) addressed the problem of intergradation between extimus and adastus explicitly. He found that in Utah there is a fair-

Figure 2. Past and present breeding distribution of E. t. extimus. Crosses, localities where breeding or probably breeding extimus were recorded before 1970 but not since; dots, localities where definitely or possibly breeding extimus have been recorded since 1970. 1, South Fork of Kern River at Weldon; 2, South Fork of Kern River 18 km E of Onyx Ranch; 3, Big Morongo Wildlife Preserve; 4, Prado Basin; 5, Santa Margarita River, Camp Pendleton; 6, Santa Margarita River, 3 km NE of Fallbrook; 7, San Luis Rey River, 3 km NE of Bonsall; 8, San Luis Rey River, Lake Henshaw to La Jolla Indian Reservation; 9, Cuyamaca Lake; 10, Sweetwater Reservoir; 11, Lower Otay Lake; 12, Tijuana River Valley; 13, Rio Santo Tomas, 5 km NW of Santo Tomas; 14, Colorado River, Grand Canyon, River Miles 47 to 54; 15, Colorado River, Grand Canyon, River Mile 71; 16, 1 km E of Fort Apache; 17, South Fork of Little Colorado River near Springerville; 18, Greer; 19, Black River, White Mountains; 20, Blue River, White Mountains; 21, San Pedro River at Dudleyville; 22, Cook's Lake; 23, San Pedro River near San Manuel; 24, Gila River at Fort Thomas; 25, Gila River at Redrock; 26, Gila River at Cliff; 27, Pleasanton, San Francisco River; 28, Glenwood, San Francisco River; 29, Reserve, San Francisco River; 30, Zuni; 31, Kirtland, San Juan River; 32, Rio Chama at Chama; 33, Rio Chama at Los Ojos/Park View; 34, Canjilon, San Juan Mountains; 35, Rio Grande at Alameda; 36, Rio Grande at Albuquerque; 37, Rio Grande at Isleta; 38, Rio Grande at Los Lunas; 39, Rio Grande at Bernardo; 40, Rio Grande at La Joya; 41, Rio Grande at Bosque del Apache National Wildlife Refuge; 42, Rio Grande at Elephant Butte Marsh; 43, Rio Grande at Caballo Lake.



ly smooth cline from darker birds in the north to paler birds in the south, but that specimens from only the southern tier of Utah counties are closer to extimus than to adastus.

In Utah the subspecies occurred along the Virgin River in the St. George and Springdale areas, 3 miles south of Kanab (Behle et al. 1958), along the San Juan River, and along the Colorado River in Glen Canyon (now under Lake Powell), where the species was found nesting in 1958 (Behle 1960).

New Mexico

The taxonomy of *E. traillii* in north-central New Mexico and Colorado has not been studied in detail and probably cannot be determined without further collecting. A. R. Phillips (pers. comm.) has identified as *extimus* Willow Flycatchers that were collected in southwestern New Mexico, along the Rio Grande north to Bernardo, Socorro County, and near Farmington on the San Juan River in northwestern New Mexico. One *extimus* collected in eastern New Mexico at Boone's Draw, Roosevelt County, on 22 May 1975 was probably a migrant. I have arbitrarily used the New Mexico/Colorado line as the northern limit of *extimus* at the eastern extreme of its range, on the speculation that the transition there from *extimus* to *adastus* may be at approximately the same latitude as in Utah.

Hubbard (1970, 1978, pers. comm.) reported several breeding or probable breeding localities in New Mexico, extending east at least to the Rio Grande, south to Anthony on the Texas line. Because the current range of Willow Flycatcher in New Mexico is nearly the same as its originally known range, I have described the species' distribution there under Current Status below.

Texas

The eastern edge of the range of extimus probably lies between the Rio Grande and Pecos River in western Texas. The subspecies has been collected at Fort Hancock on the Rio Grande (Phillips 1948), in the Guadalupe Mountains (A. R. Phillips, pers. comm.), 9 miles southeast of Glenn Springs, and 15 miles northwest of Alpine, Brewster Co., and has been reported breeding in the Davis Mountains (Oberholser 1974). Wauer (1973) called the Willow Flycatcher a rare summer resident in Big Bend National Park, but cited no specific records of breeding or occurrence outside migration periods.

Sonora

Two specimens of extimus from northern Sonora (17 June 1955, 2 km south-southwest of La Casita, 37 km south of Nogales; 1 June 1952, Agua Caliente, 48 km south of Nogales; A. R. Phillips, pers. comm.) are the only evidence that Willow Flycatchers may breed in mainland Mexico.

CURRENT STATUS

I derived information on the current status and distribution of *extimus* from published literature, contract reports to government agencies, personal communication with field ornithologists active in the southwestern states, and my own field work. Localities where breeding or summering Willow Flycatchers

have been reported since 1970 are plotted as solid circles in Figure 2. The information is most complete for southern California, where intensive surveys of riparian woodlands for Bell's Vireos have resulted in discovery of a few Willow Flycatcher colonies. Still, the picture for even this area is undoubtedly incomplete. Researchers studying Bell's Vireos observed Willow Flycatchers only incidentally; several of them stressed to me that their results could not be considered exhaustive. Probably these observers' abilities to detect and identify this species varied. Nevertheless, the primary reason that so few Willow Flycatchers have been found is that there are so few left to find. The number of localities where the species is known to occur at present is only a fraction of the number of historic localities. E. t. extimus is now absent from the major areas where it formerly occurred, such as the Los Angeles basin, the Santa Ana River near Riverside and San Bernardino, and the Colorado River.

California

The largest remaining colony of *extimus* in California is on the South Fork of the Kern River near Weldon just east of Lake Isabella, Kern County. Serena (1982) reported 26 singing birds on and near the Nature Conservancy Kern River preserve in the summer of 1982. In addition, a single singing bird was reported farther upstream along the South Fork of the Kern River 18 km east of Onyx Ranch. R. Hewitt (in McCaskie 1984) reported 23 in the Weldon area in 1984. The population increased substantially, to 39 singing birds, by 1986 (Harris et al. 1987). Harris et al. suggested that this increase may be due to the recovery of the vegetation since the Nature Conservancy acquired the area and reduced cattle grazing.

At Big Morongo Wildlife Preserve in southwestern San Bernardino County Cardiff et al. (1982) found one nesting pair in 1981. In the seven years from 1977 to 1983 that Cardiff et al. censused breeding birds at this locality, however, they found Willow Flycatchers in only that one year.

L. R. Hays (in McCaskie 1986) reported four pairs in the Prado Basin, Riverside County, in 1986. This constitutes the only report from the Santa Ana River, a former center for the species, in over 30 years.

All other localities where Willow Flycatchers summer in southern California are in San Diego County. The largest population is on the Santa Margarita River in Camp Pendleton, where L. Salata (pers. comm.) has kept careful notes on the Willow Flycatchers he has observed incidentally during his work on Bell's Vireos from 1981 through 1986. He recorded 5 territorial birds in 1981, 10 in 1982, 10 in 1983, 16 in 1984, 15 in 1985, and 17 in 1986. This apparent increase in the population size at this site coincides with the years in which Brown-headed Cowbirds (Molothrus ater) were trapped there.

The other major Willow Flycatcher colony in southern California, which R. Higson and I discovered in 1984, is along 10 km of the upper San Luis Rey River between Lake Henshaw and the La Jolla Indian Reservation. Higson (pers. comm.) searched this entire section of river on 31 May 1984 and located 12 territorial birds. Goldwasser (pers. comm.), during a survey for Bell's Vireos on 15 May 1986, detected six singing Willow Flycatchers in this area.

All other Willow Flycatcher colonies in southern California are small and apparently occupied only intermittently. Along the Santa Margarita River 3 km northeast of Fallbrook, a short distance upstream from Camp Pendleton,

S. Goldwasser (pers. comm.) found two singing birds 2 June-12 July 1980; I did not find any there on 8 and 9 May 1984 and there have been no subsequent reports from this locality. Goldwasser also found one singing bird along the lower San Luis Rey River 3 km northeast of Bonsall 4-25 June 1978. Again, I did not find any Willow Flycatchers at that locality on 7 May 1984 and there are no other reports.

On 5 June 1984 I found three singing Willow Flycatchers, plus a silent bird collecting nest material, at the south end of Lake Cuyamaca. I did not find any there, however, on 4 May and 28 June 1986. Eight egg sets of this species had been collected at this locality in 1920 and 1921.

E. Copper (pers. comm.) found two territorial Willow Flycatchers at the upper end of Sweetwater Reservoir in 1984. But the only observation there in 1986 was of a single singing bird on 9 July (J. Griffith, pers. comm.). Two egg sets were collected at Sweetwater Reservoir in 1920 and 1921.

I found one singing Willow Flycatcher on Jamul Creek at the east end of Lower Otay Lake on 13 July 1975, but this habitat was later flooded by the rising level of the reservoir. Although suitable habitat has regenerated, no Willow Flycatchers have been reported subsequently from that locality.

The Willow Flycatcher population in the Tijuana River Valley increased from one territorial bird in 1981 to two in 1982 to five on 9 June 1984 (G. McCaskie, pers. comm.). McCaskie found no Willow Flycatchers during a visit to part of the habitat there on 22 June 1986, however. Riparian woodland suitable for breeding Willow Flycatchers has developed along the Tijuana River only since the late 1970s, so occurrence of the species there indicates that it still has the potential to colonize new localities.

Baja California

Outside of southern California, available information on the current distribution of *extimus* is very sketchy. During a two-day trip to several tracts of riparian woodland in northern Baja California, M. Evans, P. Fromer, and I found only a single singing individual, along the Rio Santo Tomas 5 km northwest of the town of Santo Tomas on 21 June 1986. Particularly in comparison to our finding of 21 territorial Bell's Vireos during this same survey, it is clear that Willow Flycatchers are extremely rare in Baja California.

Nevada/Utah

I have no recent information from southern Nevada.

W. H. Behle (pers. comm.) states that no recent information is available on the species' status in southern Utah. He notes that the Willow Flycatcher was always rare in that region and believes that a recent change in status is likely only along the Virgin River in the vicinity of St. George, where riparian habitat has been lost to urban development. Some habitat along the Colorado River in southeastern Utah was lost by the creation of Lake Powell, but Behle believes that suitable habitat still persists along tributaries.

Arizona

Probably the steepest decline in the population levels of extimus has occurred in Arizona, though the subspecies was always localized and uncom-

mon there. The largest known colony occurs along the Colorado River in the upper Grand Canyon, where B. T. Brown (Brown and Johnson 1985, 1987; Brown et al. 1985) found two pairs in 1982, four in 1983, four in 1984, eight in 1985, and 11 in 1986. The Grand Canvon birds occur in two areas: between River Miles 47 and 54, about 24 km above the confluence of the Colorado and the Little Colorado rivers (9 pairs in 1986) and at River Mile 71 (2 pairs in 1986). Along the San Pedro River in 1985. W. C. Hunter (pers. comm.) located at four singing birds at Dudleyville and three at San Manuel, plus one nesting pair and two apparently unmated singing birds on the Gila River at Fort Thomas. One pair summered at Cook's Lake, 5 miles south of Dudleyville, in 1978 and 1979, but the species was absent there in 1986 (W. C. Hunter, pers. comm.). According to Hunter (pers. comm.). a small population probably persists in the White Mountains, since the birds have been seen recently in summer along the south fork of the Little Colorado River near Springerville, along the Black and Blue rivers, and at Greer. A. M. Rea collected one extimus 1/2 mile east of Fort Apache on 29 May 1972 (AMR 3915), but no more recent information is available from the White River. Further exploration is needed, but it is clear that extimus has been extirpated from much of the area from which it was originally described, the riparian woodlands of southern Arizona.

New Mexico

Most of the remaining population of extimus breeds apparently in New Mexico. The largest known population lives along the upper Gila River in southwestern New Mexico, where Montgomery et al. (1985) in 1983 found 19 pairs or singing birds along 3-km section of river near Redrock and 53 along an 8-km section near Cliff. Egbert (1981) found 28 and 50, respectively, in these same areas in 1981, though some of these may have been migrants. J. P. Hubbard and G. Monson (pers. comm.) found a nesting pair at Glenwood, San Francisco River valley, on 10 July 1972, and Hubbard (1970 and pers. comm.) cites Pleasanton and Reserve as additional breeding localities on this river. "Small numbers" were reported at Zuni, McKinley County, from 21 June to 27 July 1982 and two or three were there in the summer of 1984 (J. Trochet in Hubbard 1982, 1984); the species has now been confirmed as breeding there. Schmitt (1976) found the species at Kirtland, San Juan River (five on 15 July 1971), and collected on 28 July 1972 a female that had recently finished breeding. Near the Colorado line, Willow Flycatchers occur along the Rio Chama in the Chama and Los Ojos/Park View areas (Hubbard and Hundertmark, pers. comm.) and near Canjilon in the San Juan Mountains (one on 20 June 1982, Hubbard 1982).

Willow Flycatchers summer in small numbers at many places along the Rio Grande from Alameda (and at least formerly, Dixon; Hubbard pers. comm.) south. Hink and Ohmart (1984) reported eight probably breeding pairs along the middle Rio Grande in 1981 and 1982. According to W. H. Howe (pers. comm.), this report is based on observations of one singing bird at Albuquerque in 1981, two or three at Isleta in both 1981 and 1982, one at Los Lunas in 1981, and four at La Joya in 1982. C. A. Hundertmark (pers. comm.) found two singing Willow Flycatchers at Oxbow Marsh, Albuquerque, on 6 July 1985 and one on 7 June 1986. Howe (pers. comm.) found two singing

3 miles north of Bernardo on 20 June 1983 but noted that the birds were absent from La Jova in 1986 and that the habitat there had been dredged by the local water conservancy authority. Farther south along the Rio Grande, summering Willow Flycatchers have occurred recently at Bosque del Apache National Wildlife Refuge (one 6-26 June 1982, D. and S. Huntington in Hubbard 1982) and Caballo Lake (J. P. Hubbard, pers. comm.). At Elephant Butte Marsh, Hundertmark (1978) found 10 nests or family groups in 1974. six in 1975. The tract where these Willow Flycatchers occurred has since been flooded by rising water levels, and although additional suitable habitat has grown farther upstream, Willow Flycatchers were not relocated there during surveys conducted from 1979 to 1981 (C. A. Hundertmark, pers. comm.). The Willow Flycatcher may now be absent from the Rio Grande in Dona Ana County, where it nested at Radium Springs and Anthony (Hubbard 1970) and was collected at Las Cruces (A. R. Phillips pers. comm.) but has not been reported recently. Hubbard (1970, 1978) lists several other New Mexico localities as possible breeding sites or as sites of records needing further substantiation (not plotted in Figure 2).

Hubbard (pers. comm.) believes the species' status in New Mexico has not changed in recent years and that the population there may number several hundred pairs. He notes that many tracts of suitable habitat remain uninvestigated, however.

Summary

On the basis of the maximum population counted in any year at each of the 10 sites, the known Willow Flycatcher population in the California range of extimus consists of 87 pairs. Because so much of the riparian woodland of this area has been surveyed in recent years, I believe this number represents a substantial majority of the actual population. The population in Arizona cannot be more than a few dozen pairs and may be less. Even if a few hundred pairs persist in New Mexico, the total population of the subspecies is well under 1000 pairs; I suspect 500 is more likely. Although the data reveal no trend during the past few years, the population is clearly much smaller now than 50 years ago, and no change in the factors responsible for the decline seems likely.

GENERAL BIOLOGY

Migration Schedule

Proper field studies of Willow Flycatchers require an understanding of the species' migration. The northwestern race *E. t. brewsteri* is far more numerous than *extimus* and is common in migration in the western part of the latter's range. *E. t. brewsteri* is one of the latest spring migrants in western North America, not arriving until about 15 May. The earliest specimens I have identified were collected on 7 May (1908, near Cabazon, MVZ 1686) and 11 May (1906, Ventura, MVZ 6898). Peak numbers pass through southern California around 1 June, and Garrett and Dunn (1981) state that Willow Flycatchers are still migrating north until about 20 June. The latest spring date on which I have identified *brewsteri* in the California range of *extimus* is 13 June (1953, 6 miles southwest of Niland, SBCM 31042), but Phillips et al.

(1964) reported a brewsteri collected in Arizona on 23 June (1932, Bates Well, Organ Pipe Cactus National Monument). Fall migrant brewsteri arrive in southern California by 18 July (1908, near Colton, MVZ 3184). This date may seem inordinately early for fall migration of a land bird, but is in fact no earlier than the beginning of fall migration of such familiar species as Western Tanager (Piranga ludoviciana) and Black-headed Grosbeak (Pheucticus melanocephalus). Thus brewsteri is present in the range of extimus during most of the latter's breeding season, so single observations are often useless for indicating the local status of Willow Flycatchers. Any survey must encompass the period 20 June-15 July and must include repeated visits to each site to verify that any Willow Flycatchers seen are resident and territorial. Surveys for E. t. extimus must be more intensive than surveys for a sedentary species or a migratory species, such as Bell's Vireo, that is uncomplicated by large numbers of nonlocal breeders.

The spring migration of extimus is earlier than that of brewsteri. The normal arrival of extimus in both southern California and southern Arizona (Phillips et al. 1964) is the first week of May. Hubbard (pers. comm.) found apparently territorial Willow Flycatchers along the Gila River in New Mexico on 6 May in 1960 and 1961. In four out of five years L. Salata recorded a first arrival date on the Santa Margarita River in the first week of May; his average date was 6 May. In 1981 E. Copper found the Willow Flycatcher in the Tijuana River Valley on 2 May. On the basis of sight records, April arrival has been reported twice: at Potholes, Colorado River, on 28 April 1910 (Grinnell 1914) and at Weldon on 30 April 1977 (McCaskie 1977). The Grand Canyon population, near the northern edge of the subspecies' range, is an exception to this pattern; B. T. Brown (pers. comm.) has found that breeding Willow Flycatchers do not arrive there until 15 May.

Vocalizations

Territorial Willow Flycatchers are most easily located by their songs, the notorious "witch-pew" (usually rendered "fitz-bew") and a less frequent but equally characteristic "brrrit!" My very limited observations suggest that only early to mid morning is a suitable time for counting extimus. Near Weldon on 15 May 1984 I counted from one bird 52 songs between 0805 and 0815 and 56 between 0935 and 0945, but only four between 1105 and 1115 and none between 1515 and 1525. A secondary peak of singing occurs near dusk (S. A. Laymon pers. comm.).

Willow Flycatchers begin singing in spring as soon as they arrive on their breeding territories, but stop singing in July, well before their fall departure. I found the birds still present but not singing on the San Luis Rey River on 26 July 1986. L. Salata (pers. comm.) finds that the frequency of singing on the Santa Margarita River drops after about 15 July, and B. T. Brown (pers. comm.) does not believe that Willow Flycatchers can be located reliably by song after 1 July.

Any accurate survey of Willow Flycatcher populations must accommodate the birds' singing frequency with respect to both time of day and time of year. Uncertainty in song frequency as much as uncertainty in occurrence of migrants demands that accurate censuses include repeated visits to each colony site.

Migrating Willow Flycatchers rarely sing in southern California, contra Scott (1983). For example, between 1 and 10 June 1977, when I visited Point Loma, San Diego County, and saw migrant Willow Flycatchers almost daily, I did not hear a single song. This is one of the few factors that simplifies interpretation of Willow Flycatcher observations. A bird heard singing repeatedly is probably on its breeding territory. Still, migrants do sing occasionally. This possiblility must be considered especially in May because male Willow Flycatchers tend to migrate before females. In northern California, migrants apparently sing more frequently (T. Manolis pers. comm.), possibly reflecting increasing hormone levels as the birds approach their breeding grounds.

Reproductive Biology

The following data on nesting season, clutch size, and nest placement are based largely on the egg collections in WFVZ, SBCM, and UA. Most sets from the range of extimus were from the coastal slope of southern California; 35 were from the Colorado River, and one was from Fairbank, upper San Pedro River, Arizona. On the basis of 187 dated sets, extimus usually begins nesting about 1 June. The sets range in date from 24 May to 30 July; the mean date is 16 June. In coastal California, the complete clutch consists of either three or four eggs; 60% of the sets had three eggs, 40% had four. On the Colorado River, average clutch size is smaller: of 28 unparasitized sets with clutch size recorded, 18% had two eggs, 82% had three eggs, and none had four.

The usual natural nest site for extimus is the fork of a willow. Of 172 nests whose site was specified, 148 (86%) were in willows (Salix spp.), 7 (4%) were in nettles (Urtica dioica), 4 (2%) were in grapevines (Vitis girdiana), 3 (2%) were in blackberry vines (Rubus ursinus), 3 (2%) were in unidentified vines, 3 (2%) were in alders (Alnus rhombifolia), 2 (1%) were in arrowweed (Pluchea odorata), 1 (0.5%) was in a sycamore (Platanus racemosa), and 1 was in a rosebush (Rosa californica). In New Mexico, Hubbard (pers. comm.) has found the species nesting predominantly in Salix gooddingii. At least in the eastern part of its range, however, the subspecies may now be adapting to the tamarisks (Tamarix spp.) that are replacing the natural vegetation in desert riparian areas. B. T. Brown (pers. comm.) has data suggesting that Willow Flycatchers in the Grand Canyon select tamarisks for nest sites in preference to native vegetation, and Hundertmark (1978) found that the species nested predominantly in tamarisks at Elephant Butte Marsh, New Mexico.

The elevation of the nest above the ground is quite variable, ranging from 0.6 m (2 feet) to 5.5 m (18 feet). The mean nest height is 2.3 m with a standard deviation of 0.92 m. Although the flycatchers nest exclusively in trees or in vegetation under trees, marsh plants such as cattails (*Typha* spp.) are often part of their territories and foraging habitat.

Cowbird Brood-Parasitism

Brown-headed Cowbirds, which invaded coastal southern California between 1910 and 1920, were parasitizing extimus heavily by the 1930s. W. C. Hanna (in Willett 1933) reported that it was "now difficult to find a nest

of this flycatcher, near Colton [San Bernardino Co.], that does not contain at least one egg of the Dwarf Cowbird." On the card accompanying an egg set he collected at the Santa Clara River mouth, Ventura Co., on 11 July 1937, M. C. Badger noted that cowbird eggs were "nearly always found in nests of this species."

Cowbirds have been present throughout recorded history in most of the range of *extimus* from the Colorado River eastward. Yet only two of 34 nests collected in 1902 near Yuma had been parasitized, and in New Mexico, only four of 21 nests found by Hubbard (pers. comm.) had been parasitized. Broodparasitism by cowbirds undoubtedly has played some part in the decline of *E. t. extimus*, but its relative contribution and the ways, if any, that the flycatchers have adapted to parasitism remain unknown.

OUTLOOK

The available evidence indicates that the population of *extimus* has declined precipitously and that the subspecies is now rarer than many other birds formally designated as endangered. The subspecies is now absent from many areas were it was once common, and most of the remaining population is restricted to a few colonies. Even in New Mexico, where the largest numbers persist, the Willow Flycatcher's continuing survival is threatened by progressive loss of riparian habitat, especially the marshy situations the birds use most extensively (J. P. Hubbard, pers. comm.).

Riparian habitat destruction is probably most responsible for the decline of extimus. For example, the water conservancy authority along the middle Rio Grande regularly dredges out the willow thickets in drainage channels where the flycatchers occur, at a minimum forcing the birds to shift frequently from site to site and leaving no opportunity for population recovery (W. H. Howe, pers. comm.). Several of the colony sites are threatened by proposed reservoirs. Recent bird surveys that have located Willow Flycatcher colonies, such as those of Montgomery et al. (1985) and Hink and Ohmart (1984), were prompted by proposals for dams whose construction would inundate extensive riparian zones. Protection and restoration of riparian woodland is clearly the flycatchers' primary need, but their basic biology, particularly habitat requirements and response to cowbird parasitism, must be known better before specific management practices can be adopted.

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